

University of Groningen

Scoring abdominal profiles to characterize migratory cohorts of shorebirds

Wiersma, Popko; Piersma, Theunis

Published in:
Journal of Field Ornithology

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
1995

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Wiersma, P., & Piersma, T. (1995). Scoring abdominal profiles to characterize migratory cohorts of shorebirds: An example with Red Knots. *Journal of Field Ornithology*, 66(1), 88-98.

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.



WILEY

Scoring Abdominal Profiles to Characterize Migratory Cohorts of Shorebirds: An Example with Red Knots (Registrando Perfiles Abdominales Para Caracterizar Cohortes de Aves Playeras Migratorias: Un Ejemplo en *Calidris canutus*)

Author(s): Popko Wiersma and Theunis Piersma

Source: *Journal of Field Ornithology*, Vol. 66, No. 1 (Winter, 1995), pp. 88-98

Published by: [Wiley](#) on behalf of [Association of Field Ornithologists](#)

Stable URL: <http://www.jstor.org/stable/4513986>

Accessed: 27/06/2013 08:13

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Association of Field Ornithologists and Wiley are collaborating with JSTOR to digitize, preserve and extend access to *Journal of Field Ornithology*.

<http://www.jstor.org>

SCORING ABDOMINAL PROFILES TO CHARACTERIZE MIGRATORY COHORTS OF SHOREBIRDS: AN EXAMPLE WITH RED KNOTS

POPKO WIERSMA

Zoological Laboratory
University of Groningen
P.O. Box 14

9750 AA Haren, The Netherlands

THEUNIS PIERSMA

Zoological Laboratory
University of Groningen
P.O. Box 14

9750 AA Haren, The Netherlands and
Netherlands Institute for Sea Research (NIOZ)
P.O. Box 59

1790 AB Den Burg, The Netherlands

Abstract.—This paper explores whether the visual scoring of abdominal profiles can be used to evaluate variation in energy stores of shorebirds. Carcass analyses showed that the mass of fat in the abdominal cavity is well correlated with total fat mass and body mass. In May 1990, abdominal profiles were scored of Red Knots (*Calidris canutus*, subspecies *canutus*) on their last spring staging area in northern Germany before the 4000–5000-km long flight to the Siberian-arctic breeding grounds. Scores made in the field varied between 1 (concave shape of abdomen) to 5 (bulging). Average abdominal profile scores increased significantly over time in May 1990, paralleled by an increase in body mass, as based on catches of Red Knots in earlier years. At the end of May the average abdominal profile decreased, presumably due to the departure of adult Red Knots, leaving lean, perhaps mainly immature, birds behind. The scale of abdominal profile scores is probably too coarse to estimate fat content of individual waders. On a cohort level, however, the measure has much potential for comparisons of (re-)fuelling rates between different groups, feeding areas and years without the need to obtain large samples of captured birds.

REGISTRANDO PERFILES ABDOMINALES PARA CARACTERIZAR COHORTES DE AVES PLAYERAS MIGRATORIAS: UN EJEMPLO EN *CALIDRIS CANUTUS*

Sinopsis.—Se discute si el registro visual de perfiles abdominales puede usarse para evaluar variaciones en la energía almacenada por aves playeras. Los análisis de restos muestran que la masa de grasa en la cavidad abdominal está bien correlacionada con la masa total de grasa y con la masa corporal. En mayo del 1990, se registraron los perfiles abdominales de individuos de *Calidris canutus canutus* en su última parada primaveral en el norte de Alemania antes del vuelo de 4000 a 5000 km que les lleva a las áreas de reproducción en la zona ártica Siberiana. Anotaciones hechas en el campo variaron entre 1 (abdomen de forma cóncava) y 5 (abdomen protuberante). Los promedios de anotaciones sobre los abdómenes aumentaron significativamente a través del tiempo en mayo 1990, junto a un aumento en masa corporal, tal como se observa en colecciones de individuos de la especie en años recientes. El promedio del perfil abdominal disminuyó a fines de mayo, posiblemente debido a que los individuos adultos migran y dejan atrás las aves delgadas, principalmente juveniles. La escala para evaluar los perfiles abdominales es probablemente demasiado burda para estimar el contenido de grasa de los individuos. Sin embargo, a nivel de cohorte esta medida tiene mucho potencial para comparar tasas de reabastecimiento entre diferentes grupos, áreas de alimentación y años sin tener que capturar grandes grupos de aves.

During the storage period before a long distance flight, fat can be deposited at many different sites in the bird's body (Pond 1978), but most fat is stored subcutaneously (Blem 1976). The interfurcular region and the abdominal cavity in particular contain large amounts of fat (Blem 1976, Prater 1975). The size of these deposits is well correlated with total fat mass (Piersma 1988, Rogers 1991, Thomas et al. 1983). Therefore, useful estimates of total fat content can be obtained by visual inspection of the interfurcular and subcutaneous fat layers of birds in the hand (Kaiser 1993, Kremetz and Pendleton 1990). In larger bird species fat content can also be estimated from a distance. Owen (1981:229) used the abdominal profile as an index for the fat content of individual, free-living, Barnacle Geese (*Branta leucopsis*) and concluded that "the index gives a good guide to the condition of geese in winter and spring." Since then, abdominal profiles have been used by other waterfowl workers in Europe: Amat et al. (1991), Loonen et al. (1991), and Van Eerden et al. (1991) on Greylag Geese (*Anser anser*); Mayes (1991) on White-fronted Geese (*Anser albifrons*); Black et al. (1991) on Barnacle Geese; R. H. Drent and coworkers (pers. comm.) on Barnacle and Brent Geese (*B. bernicla*); J. H. Beekman and M. R. van Eerden (pers. comm.) on Bewick's Swans (*Cygnus columbianus bewickii*).

Shorebirds (Charadrii) store large amounts of fat prior to long-distance migrations (Drent and Piersma 1990, Evans and Davidson 1990), sometimes almost doubling in mass (Johnson 1985). Abdominal profiles of shorebirds could in principle function as an index for nutritional condition, indexing the size of the energy stores, as in geese. Here we investigate whether visual scoring of abdominal fat stores may yield useful information on the nutritional condition of shorebirds. We present results of a study on a medium-sized species, the Red Knot (*Calidris canutus*), one of the most spectacular long-distance migrants of them all (Piersma and Davidson 1992).

METHODS

Field observations.—Field observations were carried out in May 1990 near Westerhever (54°26'N, 8°38'E), on the Eiderstedt Peninsula in the German part of the Wadden Sea. We scored abdominal profiles of migrating Afro-Siberian Red Knots (*C. c. canutus*). This subspecies winters in West Africa and breeds on high arctic tundra in west or central Siberia (Piersma et al. 1992). During their spring journey, the German Wadden Sea is used as their main stop-over area. Here, from early May to early June, over 200,000 Red Knots replenish their fuel reserves (Prokosch 1988). In the beginning of May the *islandica* Red Knots depart, leaving Red Knots of the *canutus* subspecies behind (Prokosch 1988).

Abdominal profiles of individual birds in a flock were scored from a distance of about 100 m using a telescope. Scores varied from 1 to 5 (Fig. 1). A score of 1 was given to a bird that was very lean, with an abdomen more or less concave. A score of 3 was given when the abdomen was slightly convex and a score of 5 when the abdomen was bulging. Scores

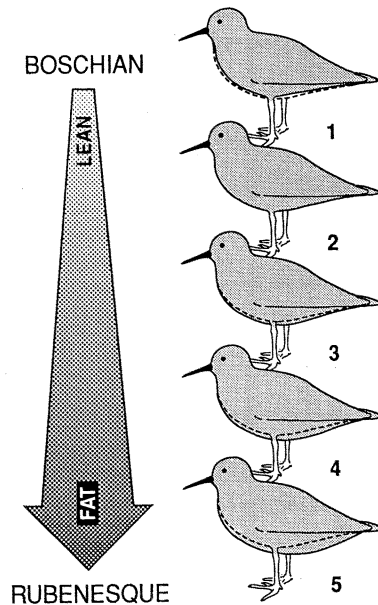


FIGURE 1. Typology of abdominal profiles of Red Knots as scored in the field, ranging from 1 (very lean) to 5 (very fat). As an associative learning aid, we have suggested Flemish painters indicative of the different profile styles.

of 2 and 4 were given to intermediate profiles. Juvenile birds, as based on plumage characteristics, were left out of the analysis.

On 23 May 1990, abdominal profile indices of eight adult Red Knots caught near Westerhever were estimated while held in the hand, allowing abdominal-profile score to be correlated with body mass among individuals. Besides visual clues, no prior knowledge of their body masses was available to the observer.

Before breeding, adult Red Knots molt from a greyish non-breeding plumage to a rusty-red breeding plumage. They start body molt in the African wintering areas 2 mo before arrival at the spring staging sites (Piersma 1989, Zwarts et al. 1990). The plumage composition was followed throughout the field study period. We scored individual birds, including the birds for which abdominal profiles were scored, according to five plumage categories: full summer, $\frac{3}{4}$ summer, $\frac{1}{2}$ summer, $\frac{1}{4}$ summer and non-breeding. Only the proportions of full summer and non-breeding plumages are discussed in the text.

Fat extractions.—Thirty-six freshly found carcasses of Red Knots originating from the Wadden Sea (lighthouse victims), from Iceland (catching casualties) and from birds held in captivity for various lengths of time (minimum 6 mo), were analyzed for fat content (see Piersma et al. 1993). Captive birds were included in order to enlarge the data set, but we payed

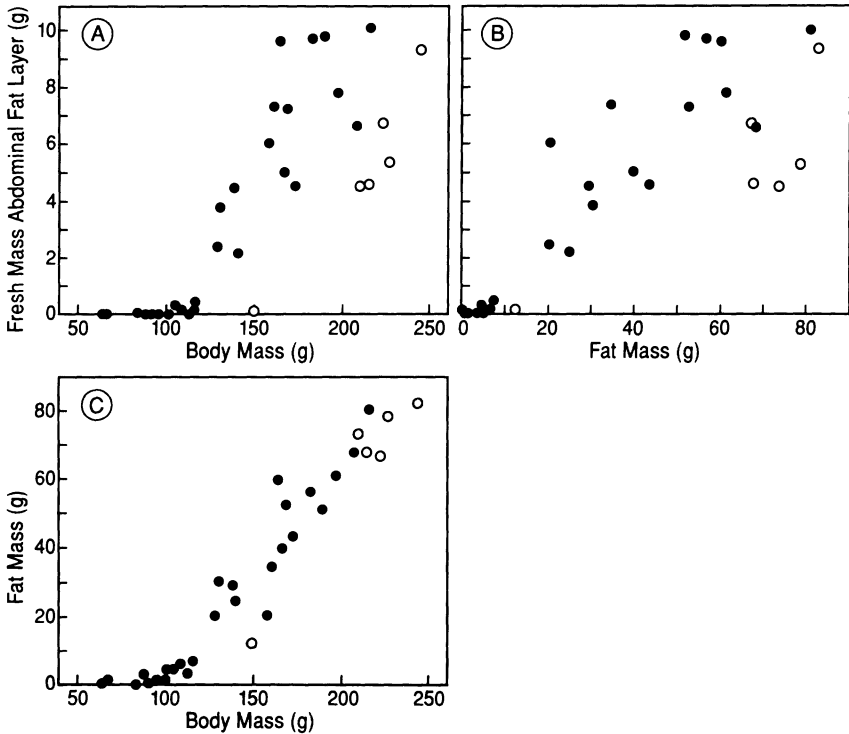


FIGURE 2. Fresh abdominal fat mass of Red Knots relative to fresh body mass (A), relative to the total extracted fat mass (B), and total extracted fat mass relative to fresh body mass (C). Most birds were held in captivity for at least 6 mo before being sacrificed (filled circles) and few were freshly from the wild (open circles).

attention to the correspondence between wild and captive birds in the fat variables. Most of the birds belonged to the *islandica* subspecies of Red Knot (see Davidson and Wilson 1992), but because *canutus* and *islandica* show complete overlap in internal dimensions and condition-related variables (unpubl. data), this should not have biased the outcomes. The carcasses were preserved at -20°C . Before dissection the birds were thawed and weighed. The clearly separable layer of abdominal fat, lying ventral and posterior of the stomach and around the intestines (see Pierisma 1984, Woodall 1978), was taken out and weighed freshly (abdominal fat mass). After the dissected material had been dried at $50\text{--}70^{\circ}\text{C}$ to constant mass, net abdominal fat mass and total fat mass were measured by fat extraction using petroleum-ether (boiling traject $40\text{--}62^{\circ}\text{C}$) in a Soxhlet apparatus.

RESULTS

Fat extractions.—Abdominal fat mass was strongly correlated with body mass ($r = 0.81$, $n = 36$, $P < 0.0001$; Fig. 2A) and with total fat mass (r

= 0.88, $n = 36$, $P < 0.0001$; Fig. 2B). The amount of abdominal fat increased with body masses over 110 g; below this mass no abdominal fat was apparent (Fig. 2A). Body mass consisted of up to 6% abdominal fat (approx. 10 g).

The variation in body mass in birds weighing less than 110 g was related to age and not to fat content, because total fat mass in these birds was about 1 g. The lightest birds were all juveniles. Regression of body mass on total fat mass and age (0 or 1) significantly includes both variables ($r = 0.97$, $n = 36$, $P < 0.0001$). For similar fat masses, adults were 21 g heavier than juveniles (t -test on regression coefficient of age, $t = 3.3$, $P < 0.05$), implying them to have a bigger musculature and/or internal organ size. Wild birds had an estimated 6 g less fat in the abdominal cavity than captive birds with the same body mass (comparison of origins of regression equations of abdominal fat with body mass, after transformation of the x-axis so that the origins fall within with range of the data: $n = 19$ and 6 for captive and wild birds, respectively, $t = 18$, $P < 0.0005$; Fig. 2A). Body mass was strongly correlated with total fat mass (Fig. 2C; see Van der Meer and Piersma 1994). This relationship seemed to hold for wild birds as well, but only six of these were measured (Fig. 2C).

Fresh abdominal fat did not entirely consist of fat. Above an abdominal fat mass of 0.5 g, the fraction of dry fat was constant at 93% ($r = 0.04$, $n = 15$). Below 0.5 g the fat content steeply decreased ($r = 0.77$, $n = 16$, $P < 0.0005$), which supports the idea that the abdominal fat is deposited in an already existing fat-free tissue, which is filled up and then expands (Blem 1976, Johnston 1973).

Field observations.—The frequency distributions of abdominal fat scores in May 1990 are compared with the average body masses of adult Red Knots captured in the same area and the same time of year during several preceding years (Fig. 3) (data from Prokosch 1988: Table 16, supplemented with data from eight adult Red Knots caught during May 1990). This comparison is valid since average body mass of Red Knots captured in May in different years are highly comparable, if date is controlled for (regression analyses of daily average body masses in different years against day in May: $r = 0.90$, $n = 11$, $P < 0.0005$; unpubl. data). The residual deviations range between -13 and 16 g. In the course of the season the abdominal profile scores increased, as did body mass. Average abdomen profile score and body mass on matching dates are combined in Fig. 4. This yields a significant positive correlation ($r = 0.80$, $n = 8$, $P < 0.05$). Note that only data collected after 11 May were included to avoid mixing data from two subspecies.

On 23 May 1990 abdominal profile scores and body mass measurements were done on eight freshly caught adult Red Knots held in the hand (Fig. 4). Body mass correlated significantly with abdominal profile ($r = 0.97$, $P < 0.0005$). Because the posture of a bird in the hand is totally different from that of a free-living bird, results of the two methods cannot be compared quantitatively.

The proportion of birds in breeding plumage was high throughout

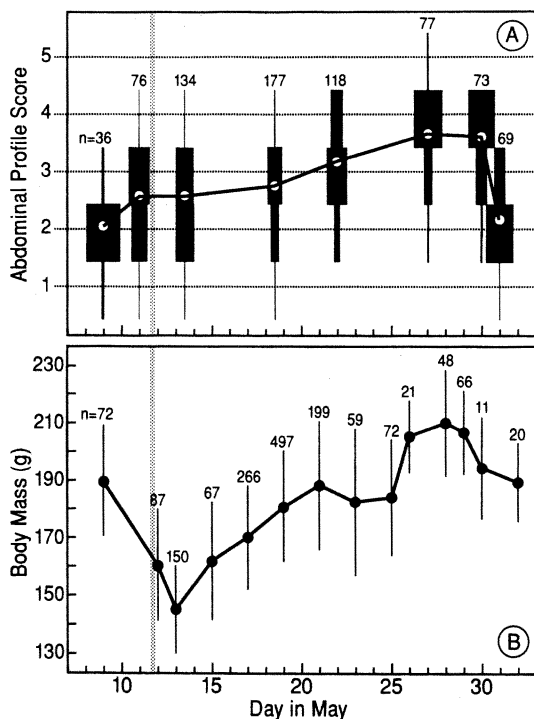


FIGURE 3. Change in the condition of Red Knots staging in the Westerhever area in Germany in May. During the first 4 d (dashed lines) the *islandica* and *canutus* subspecies can occur next to each other, but most adult *islandica* Red Knots will have left thereafter (Prokosch 1988). A) Frequency distributions of abdominal profile scores during pre-migratory fattening in May 1990. Red Knots in complete winter plumage (supposedly juveniles) were left out of the analysis. Profile scores are as depicted in Figure 1. The lines connect average values and numbers indicate sample sizes. B) Average body masses with standard deviations of adult Red Knots in May, captured in the same area during several preceding years (data from Prokosch 1988, Table 16, supplemented with eight adult Red Knots caught during May 1990). Sample sizes are indicated in the figure, and only samples larger than five are incorporated.

May. On 31 May, however, the final day of observation, flocks were observed with only a few Red Knots in breeding plumage (Fig. 5). This coincided with observations of Red Knots departing for the breeding grounds (Piersma et al. 1991) and a sudden decrease in average abdominal profile score (Fig. 3A).

A comparison of the frequency distribution of body mass with abdominal profile scores in two periods in May showed great overlap in relative range as well as in shape (Fig. 6). To make the comparison more direct, we calculated the expected frequency distribution of abdominal profile scores from the body mass distribution (Fig. 6), assuming complete overlap of the x-axes of the abdominal profile score and body mass as shown

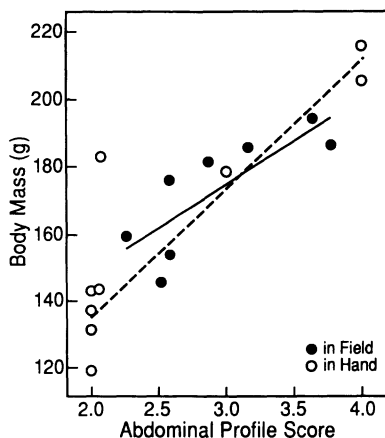


FIGURE 4. Relationship between the average profile scores, as shown in Figure 3A, and body mass, shown in Figure 3B ("in field"). For dates that we obtained abdominal profile scores but no body mass data were available, masses were interpolated. Only data gained after 11 May were included; in the latter period no adult *islandica* Red Knots were present. The open circles show abdominal profile scores of wild adult Red Knots, held in the hand, relative to their fresh body mass ("in hand"). The birds were caught near the study area on 23 May 1990.

in the figure. Again, shape and range show visual agreement, although in the first period the two distributions differ statistically (Kolmogorov-Smirnov test, $D_{110,262} = 0.23$ $P < 0.05$), while in the second period they do not ($D_{93,87} = 0.15$, $P = 0.25$). We conclude that abdominal profiles reflect the actual distribution of body masses in the population.

DISCUSSION

Although more data on fat content of captive Red Knots was available than of wild birds, the relationships between abdominal fat mass, fat mass and body mass are qualitatively comparable (Fig. 2). The remaining divergence of fat contents of wild and captive birds can be explained by a decrease in the size of the digestive tract in aviary birds (Piersma et al. 1994). As abdominal profiles are well correlated with body mass on a seasonal and individual basis (Fig. 4), and as abdominal fat mass is well correlated with total body mass (Fig. 2A) and total fat mass (Fig. 2B), abdominal profile scores can be used to estimate the nutritional condition of Red Knots. Intervals between the visual scores represent considerable mass differences. One interval equals 25–40 g (Fig. 4). Such an interval does not allow detailed estimates of total fat mass of individual birds. Additionally, the abdominal-profile scale is not necessarily linearly correlated with body mass over the whole range of values. The variation in scores per day also seems big (Fig. 3A). As body mass also covers a large range of values, the range in abdominal scores appears a good reflection

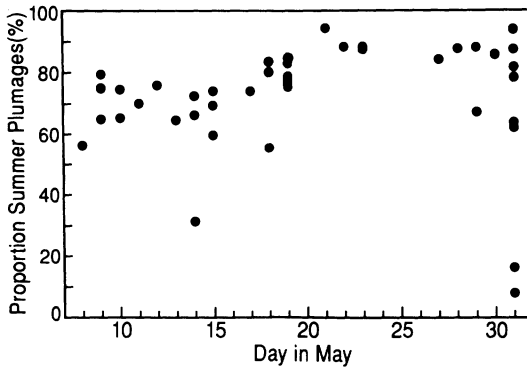


FIGURE 5. Proportions of Red Knots in full breeding plumage in different flocks during May 1990 in the Westerhever area in Germany. Sample sizes 99–1547.

of real inter-individual condition differences rather than reflecting inaccuracies in abdominal profile estimates.

Visual fat scores may, therefore, provide a useful measure to evaluate the function and quality of staging sites where cohorts of species, which differ in the location of wintering areas or breeding grounds and the timing of migration, gather. In the German Wadden Sea, for example, heavy Red Knots are replaced by lean Red Knots in the beginning of May, indicating the departure of the *islandica* subspecies and the arrival of *canutus* Red Knots (Piersma et al. 1991, Prokosch 1988). The observed drop in average abdominal profile score on the last day of May (Fig. 3A), coincided with observations of departing Red Knots (probably the fattest) on 28, 29 and 30 May (Piersma et al. 1991). This was confirmed by the low proportion of breeding plumages on 31 May (Fig. 5), presumably flocks with a high proportion of immature birds, which remain there over summer (Dick et al. 1976, Prokosch 1988).

Given appropriate checks of the consistency of observers in scoring abdominal profiles, such profiles can be used to make comparisons between years. On staging sites where birds come together to refuel, birds can be prevented from gaining mass by depletion of food resources, e.g., through climatic changes or human interference. In comparisons of areas receiving birds of a specific cohort, abdominal profiles may be used to characterize site use and habitat quality, making it possible to discriminate between different groups of birds (e.g., migratory and non-migratory, juveniles and adults or males and females). Especially at sites where catching birds is impossible or problematic, abdominal profile scores have the advantage of being quite easily and quickly obtained. The method should be explored and exploited to a greater extent by shorebird biologists.

ACKNOWLEDGMENTS

It was a great pleasure to watch Red Knots with Ingrid Tulp and Yvonne Verkuil. We thank Peter Prokosch and Herman Hötter of the WWF-Wattenmeerstelle Schleswig-Holstein in

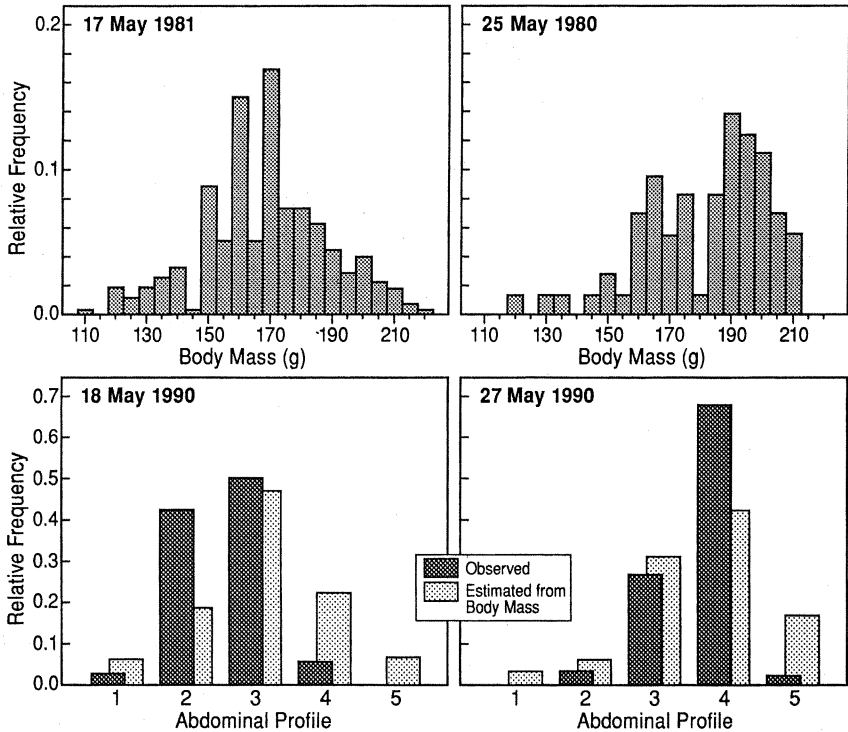


FIGURE 6. A comparison of frequency distributions of body mass of adult Red Knots (from Prokosch 1988: Fig. 53) and abdominal profile scores, mid-May and at the end of May. Body mass data of 17 May 1981 were compared with abdominal profiles scored on 18 May 1990 and a similar comparison is made between data from 25 May 1980 and 27 May 1990. The open bars in the lower panels represent the frequency distribution of body masses estimated from the distribution of abdominal profile values in the upper panels. To achieve this we assumed that the x-axes of the lower and upper panels show complete overlap.

Husum, Germany, who arranged our stay at Westerhever and who organized the bird catches. Gudmundur A. Gudmundsson brought fat birds from Iceland to Groningen and helped in analyzing them, Hans-Ulrich Rösner and Georg Nehls organized Westerhever-lighthouse victims, Annemiek Scheele and Cherry Ott helped with the practicalities of carcass analyses, Hans Schekkerman sketched Red Knots and Dick Visser prepared the final figures. We thank Yvonne Verkuil, Leo Bruinzeel, Ingrid Tulp and Nick Davidson for commenting on early drafts, Dr. Andreas Kaiser and Dr. Rob Butler for reviewing the manuscript and the editor for further help.

LITERATURE CITED

- AMAT, J. A., B. GARCIA-CRIADO, AND A. GARCIA-CIUDAD. 1991. Food, feeding behaviour and nutritional ecology of wintering Greylag Geese *Anser anser*. *Ardea* 79:271–282.
- BLACK, J. M., C. DEERENBERG, AND M. OWEN. 1991. Foraging behaviour and site selection of Barnacle Geese *Branta leucopsis* in a traditional and newly colonised spring staging habitat. *Ardea* 79:349–358.

- BLEM, C. R. 1976. Patterns of lipid storage and utilization in birds. *Amer. Zool.* 16:671–684.
- DAVIDSON, N. C., AND J. R. WILSON. 1992. The migration system of European-wintering Knots *Calidris canutus islandica*. Wader Study Group Bull. 64, Suppl.:39–51.
- DICK, W. J. A., M. W. PIENKOWSKI, M. WALTNER, AND C. D. T. MINTON. 1976. Distribution and geographical origins of Knot *Calidris canutus* wintering in Europe and Africa. *Ardea* 64:22–47.
- DRENT, R., AND T. PIERSMA. 1990. An exploration of the energetics of leap-frog migration in arctic breeding waders. Pp. 399–412, in E. Gwinner, ed. *Bird migration: physiology and ecophysiology*. Springer-Verlag, Berlin, Germany.
- EVANS, P. R., AND N. C. DAVIDSON. 1990. Migration strategies and tactics of waders breeding in arctic and north temperate latitudes. Pp. 387–389, in E. Gwinner, ed. *Bird migration: physiology and ecophysiology*. Springer-Verlag, Berlin, Germany.
- JOHNSON, C. 1985. Patterns of seasonal weight variation in waders on the Wash. *Ring. Migr.* 6:19–32.
- JOHNSTON, D. W. 1973. Cytological and chemical adaptations of fat deposition in migratory birds. *Condor* 75:108–113.
- KAISER, A. 1993. A new multi-category classification of subcutaneous fat deposits of song-birds. *J. Field Ornithol.* 64:246–255.
- KREMENTZ, D. G., AND G. W. PENDLETON. 1990. Fat scoring: sources of variability. *Condor* 92:500–507.
- LOONEN, M. J. J. E., M. ZIJLSTRA, AND M. R. VAN EERDEN. 1991. Timing of wing moult in Greylag Geese *Anser anser* in relation to the availability of their food plants. *Ardea* 79:253–259.
- MAYES, E. 1991. The winter ecology of Greenland White-fronted Geese *Anser albifrons flavirostris* on semi-natural grassland and intensive farmland. *Ardea* 79:295–304.
- OWEN, M. 1981. Abdominal profile—a condition index for wild geese in the field. *J. Wildl. Manage.* 45:227–230.
- PIERSMA, T. 1984. Estimating energy reserves of Great Crested Grebes *Podiceps cristatus* on the basis of body dimensions. *Ardea* 72:119–126.
- . 1988. Body size, nutrient reserves and diet of Red-necked and Slavonian Grebes *Podiceps grisegena* and *P. auritus* on Lake IJsselmeer, The Netherlands. *Bird Study* 35:13–24.
- . 1989. Knot (*Calidris canutus*). Pp. 264–277, in B. J. Ens, T. Piersma, W. J. Wolff, and L. Zwarts, eds. *Report of the Dutch-Mauritanian project Banc d'Arguin 1985–1986*. WIWO-report 25/RIN-report 89/6, Texel, The Netherlands.
- , AND N. C. DAVIDSON (EDS.). 1992. The migration of Knots. Wader Study Group Bull. 64, Suppl.:1–210.
- , J. VAN DER MEER, AND R. DRENT. 1994. Seasonal shifts in organ and muscle size of a long-distance migrant, the knot: a function of food type and work level? Pp. 262–272, in T. Piersma. *Close to the edge: energetic bottlenecks and the evolution of migratory pathways in knots*. Ph.D. thesis. University of Groningen, The Netherlands.
- , A. KOOLHAAS, AND A. DEKINGA. 1993. Interactions between stomach structure and diet choice in shorebirds. *Auk* 110:552–564.
- , P. PROKOSCH, AND D. BREDIN. 1992. The migration system of Afro-Siberian Knots *Calidris canutus canutus*. Wader Study Group Bull. 64, Suppl.:52–63.
- , I. TULP, Y. VERKUL, P. WIERSMA, G. A. GUDMUNDSSON, AND Å. LINDSTRÖM. 1991. Arctic sounds on temperate shores: the occurrence of song and ground display in Knots *Calidris canutus* at spring staging sites. *Ornis Scand.* 22:404–407.
- POND, C. M. 1978. Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. *Ann. Rev. Ecol. Syst.* 9:519–570.
- PRATER, A. J. 1975. Fat and weight changes of waders in winter. *Ring. Migr.* 1:43–47.
- PROKOSCH, P. 1988. Das Schleswig-Holsteinische Wattenmeer als Frühjahr-Aufenthaltsgebiet arktischer Watvogel-Populationen am Beispiel von Kiebitzregenpfeifer (*Pluvialis squatarola*, L. 1758), Knutt (*Calidris canutus*, L. 1758) und Pfuhlschnepfe (*Limosa lapponica*, L. 1758). *Corax* 12:273–442.
- ROGERS, C. M. 1991. An evaluation of the method of estimating body fat in birds by quantifying visible subcutaneous fat. *J. Field Ornithol.* 62:349–356.

- THOMAS, V. G., S. K. MAINGUY, AND J. P. PREVETT. 1983. Predicting fat content of geese from abdominal fat weight. *J. Wildl. Manage.* 47:1115–1119.
- VAN DER MEER, J., AND T. PIERSMA. 1994. Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. *Physiol. Zool.* 67:305–329.
- VAN EERDEN, M. R., M. ZIJLSTRA, AND M. J. J. E. LOONEN. 1991. Individual patterns of staging during autumn migration in relation to body condition in Greylag Geese *Anser anser* in The Netherlands. *Ardea* 79:261–264.
- WOODALL, P. F. 1978. Omental fat: a condition index for redbilled teal. *J. Wildl. Manage.* 42:188–190.
- ZWARTS, L., B. J. ENS, M. KERSTEN, AND T. PIERSMA. 1990. Moults, mass and flight range of waders ready to take off for long-distance migrations. *Ardea* 78:339–364.

Received 24 Jan. 1994; accepted 13 May 1994.